ISSN 1346-7565 Acta Phytotax. Geobot. 66 (2): 61–79 (2015)

The Taxonomy of Podostemaceae Subfamily Tristichoideae in Laos, with Descriptions of Seven New Species

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This study, based on comparative morphology reinforced by phylogenetic relationships deduced from *matK* sequences, records 15 species in three genera of Podostemaceae subfamily Tristichoideae from Laos. The species new to science are *Dalzellia attapeuensis, D. microphylla, D. pseudoangustissima, Terniopsis microstigma, T. savannaketensis, T. sesadensis,* and *T. vapyensis. Cussetia diversifolia* is excluded from the flora, although it has been reported as being in Laos. Floristic comparison by country shows a significant overlap between the Lao and Thai floras. Given not only the large number of species but also the high incidence of endemism, where seven of the 15 species are known only from within the country, Laos, together with Thailand, represents a center of diversity for Tristichoideae in Asia.

Key words: *Cussetia, Dalzellia*, hotspot, Laos, *Terniopsis,* Tristichoideae

The aquatic and lithophytic family Podostemaceae, also known as river-weeds, grows in tropical rapids and waterfalls, and comprises three subfamilies, of which Podostemoideae and Tristichoideae occur in Asia (Cook & Rutishauser 2007). For Podostemoideae, we recently recorded five genera and 15 species from Laos (Koi & Kato 2012), which is remarkably more than the previous reports of three genera and five species (Cusset 1973a, 1973b, 1992, Kato & Fukuoka 2002). However, less is known about the subfamily Tristichoideae in Laos.

The Tristichoideae comprise about 20 species in six genera worldwide, with a center of species diversity in Asia (Kato 2006, Cook & Rutishauser 2007, Koi *et al*. 2009). Two species in one genus have been recorded from Laos (Cusset 1973b, Cusset & Cusset 1988, Kato & Fukuoka 2002). In the latest classification they are recognized as *Cusseta carinata* and *C. diversifolia* (Kato 2006). The small number of species in Laos contrasts significantly with Tristichoideae in Thailand, where 13 species in 3 genera have been recorded (Kato 2006, Kato & Koi 2009, Werukamkul *et al.* 2012). This may imply that the Tristichoideae have been overlooked in Laos and therefore unrecognized or undescribed taxa are to be expected. This hypothesis is partially supported by a recent molecular phylogenetic analysis, in which several phylogenetically unique unidentified collections from Laos were detected (Koi *et al.* 2012).

The primary aim of our study was to revise the Tristichoideae in Laos. To do so, we investigated the previously known taxa and examined the morphology of Lao specimens that were to be assigned to known species or to be described as new. The Tristichoideae of Laos were then compared with the Tristichoideae in the neighboring countries of Asia and Australia.

Materials and Methods

We first studied specimens of *Cussetia*, a genus of Tristichoideae previously known in Laos, in the Herbarium of the National Museum of Natural History, Paris (P). We then examined our own collections, including recently collected specimens from northern, central and southern Laos used in a molecular phylogenetic analysis (Koi *et al*. 2012) of Tristichoideae. Those specimens, in either FAA (formaldehyde : acetic acid : 50% ethyl alcohol = 5 : 5 : 90), 70% ethyl alcohol or dried, have been deposited in the Department of Botany, National Museum of Nature and Science, Tsukuba (TNS) and in the National Herbarium of Laos (HNL). The number of species and incidence of endemism of Tristichoideae in Laos was then compared with neighboring countries, based on the reports by Lecomte (1909), Chao (1980), Cusset & Cusset (1988), Aston (1990), Mathew *et al*. (2001), Kato (2006, 2009), Kato & Koi (2009), and Werukamkul *et al*. (2012).

Results and Discussion

Taxonomy of Tristichoideae in Laos

Two species in one genus, *Dalzellia* [later transferred to *Cussetia* by Kato (2006)], of Tristichoideae were previously known to occur in Laos (Cusset 1973b, Cusset & Cusset 1988, Kato & Fukuoka 2002). Of the nearly 80 specimens of Tristichoideae that we examined from Laos, 3 belonged to *Cussetia*, 21 to *Dalzellia* and 56 to *Terniopsis*. To identify them, we have prepared a comprehensive key to the genera. We also present a summary of our phylogenetic and taxonomic insights. A few specimens not identified in this study, but referable to *Dalzellia* or *Terniopsis*, need further study.

Key to the genera of Tristichoideae in Laos

1a. Roots adhering to rock surface, subcylindrical or ribbon-like; shoots borne at flank of root, cylindrical, leafy; flower buds covered by bracts 2
1b. Root absent; instead shoots adhering to rock surface; shoots crustose or ribbon-like, with leaves on dorsal surface and at margin; flower buds enclosed by leafy cupules ..... *Dalzellia*
2a. Bracts below flower 2, membranous or thick, not carinate ..... *Terniopsis*
2b. Bracts below flower many, in 6 files, thick, carinate ..... *Cussetia*

Cussetia M. Kato in Acta Phytotax. Geobot. 57: 15. 2006.

Two species in Asia (Cambodia, Laos and Thailand); one in Laos.

Notes. Cussetia is a genus of two species that were previously assigned to *Dalzellia* (Cusset 1973b, Cusset & Cusset 1988). Due to the significant morphological uniqueness, such as the ribbon-like root and the shoot complex composed of one or more flowering shoots associated with one or more vegetative shoots and the many carinate bracts arranged in six files, they were segregated as the genus *Cussetia* (Kato 2006). In their three stamens they are more similar to *Terniopsis* with two or three stamens than to *Tristicha* with a single stamen. Despite multiple explorations in Cambodia, Laos and Thailand, no recent collections of *Cussetia* were obtained. Hence, no molecular evidence on the phylogenetic relationships of the genus is available.

1. **Cussetia carinata** (Lecomte) M. Kato in Acta Phytotax. Geobot. 57: 54. 2006—*Terniola carinata* Lecomte in Bull. Soc. Bot. Fr. 56: 96. 1909—*Dalzellia carinata* (Lecomte) C. Cusset in Fl. Cambodge, Laos & Viet-nam 14: 78, pl. 12. f. 4-7. 1973, p.p.; Cusset & Cusset in Bull. Mus. Natl. Hist. Nat., B, Adansonia 10: 173. 1988.

Distribution. Laos (Kato 2006), Cambodia (type locality, Lecomte 1909, Kato 2006).

Distribution in Laos. SOUTHERN: Champasak, Attapeu.

Notes. Cussetia carinata, described from Cambodia (Lecomte 1909), is the sole representative of *Cussetia* in Laos. It is easily distinguished from *C. diversifolia* from eastern Thailand by the short ramuli associated with the flowering shoot, reduced scale-like leaves on the associated ramuli, numerous bracts under the flower, and the reduced proximal bracts.

Specimens examined. SOUTHERN LAOS. Attopeu basin, *F.(A.)F.J. Harmand s.n.* ann. 1875-1877 (P); Se-Moun basin, *F.(A.)F.J. Harmand s.n.* ann. 1875-1877 (P); Champassak, Bassac, *F.(A.)F.J. Harmand s.n.* (as *Pierre 2313*) p.p. Feb. 1877 (P). CAMBODIA. *Julien s.n.* ann. 1874 (type, P).

Species exclusa

Cussetia diversifolia (Lecomte) M. Kato in Acta Phytotax. Geobot. 57: 16. 2006.

Notes. Cusset (1973b) reported two species from Laos (as *Dalzellia*), *Cussetia carinata* and *C. diversifolia*. *Cussetia diversifolia* was collected only in eastern Thailand, and probably does not occur in Laos. Cusset (1973b) cited two specimens from Laos, *Harmand s.n.* ann. 1875–77 from Attapeu and *Harmand s.n.* (as *Pierre 2313* p.p.) from Bassac. The former is *C. carinata* and the latter is a mixture of *C. carinata* and a species of *Terniopsis* (see Notes under *C. carinata* above). We therefore exclude *C. diversifolia*, which occurs only in Thailand, from the Tristichoideae of Laos.

Dalzellia Wight in Icon. Pl. Ind. Orient. [Wight] v. 34. t. 1919, 1920. 1852; Cusset & Cusset in Bull. Mus. Natl. Hist. Nat., B, Adansonia 10: 171. 1988, p.p.; Mathew & Satheesh in Aquat. Bot. 57: 246. 1997; Kato in Acta Phytotax. Geobot. 57: 9. 2006.

Eight species in tropical Asia [India (Southern), Laos, Sri Lanka, Thailand, Vietnam]; six species in Laos.

Notes. This genus consisted of one (or more) species distributed in Sri Lanka and southern India, four species in Thailand (Kato 2006). The present study records six species in Laos, of which three are also distributed in Thailand (Table 1). Laos thus represents the northern range edge of the distribution of the genus.

Dalzellia is morphologically defined as lacking the root and instead having adhering, flattened dorsiventral shoots with leaves dimorphic on the dorsal surface and lateral sides, leafy cupules enclosing flower buds, and rosettes of leaves on the dorsal surface of the shoot. The shoots are broadly or narrowly crustose or ribbon-like. This body plan is produced by the dorsiventral shoot apical meristem, which develops in the axil of the cotyledon in the seedling (Imaichi *et al.* 2004). The dorsiventral shoot is shared by *Indodalzellia gracilis* (Mathew, Jäger-Zürn & Nileena) Koi & M. Kato (Koi *et al.* 2009) and *Indotristicha tirunelveliana* Sharma, Karthik. & Shetty (Sharma *et al.* 1974), and the leafy cupule is shared by *Indotristicha ramosissima* (Wight) P. Royen (Rutishauser & Huber 1991). Molecular phylogeny indicates that *Dalzellia* is a sister to *Indotristicha* (Koi *et al.* 2012 ; Khanduri *et al.* 2015).

All species of *Dalzellia* from Southeast Asia form a clade sister to a part of the Indo-Sri Lankan *D. zeylanica* (Koi *et al.* 2012). Like the genetically diversified and morphologically variable *D. zeylanica* (which requires close taxonomic analysis), the Southeast Asian relatives are morphologically variable and thus recognized as the outcome of speciation, and possibly products of rapid radiation.

The phylogenetic relationships of *Dalzellia* among the Southeast Asian species are not well resolved, except for the moderately supported sister relationship of *D. kailarsenii* and *D. ranongensis*, with which a tentatively identified Lao specimen (*Dalzellia* cf. *kailarsenii*) clustered (Koi *et al.* 2012). Similarly, two unidentified specimens of *Dalziella* from Laos were placed with *D. ubonensis* from Thailand (Koi *et al.* 2012). In both cases, morphological assessments of the Lao specimens showed close similarities with the types and protologues of those two species. We therefore identified them as *D. kailarsenii* and *D. alzellia. ubonensis*, respectively (for

more details see species notes).

Some Lao specimens with a haplotype identical with the holotype of *D. angustissima* from Thailand were tentatively identified as *Dalzellia* cf. *angustissima,* while two unidentified specimens of *Dalzellia* sp. *LKF111* and *LKF123* had a unique haplotype (Koi *et al*. 2012). In contrast, the remaining five unidentified Lao specimens with three phylogenetically unique haplotypes (*Dalzellia* sp. *L-10, LK-201,* and *LKF-12*; *LK-118*; and *LK-130*) differ morphologically and are therefore described as *D. pseudoangustissima, D. microphylla,* and *D. attapeuensis,* respectively.

The distribution pattern of *Dalzellia* is noteworthy. Each locality harbors only a single species or haplotype (but occasionally harbors other genera of deep divergence, such as *Terniopsis* in Huay Banglien River, Champasak Prov. and Tad Nam Pa Waterfalls, Attapeu Prov.). In fact, of the 19 localities of *Dalzellia*, 17 are occupied by single species. In contrast, *D. angustissima* and *D. ubonensis* are sympatric in a small area in Tad Hiew Khon waterfall and *D. angustissima* and *D. attapeuensis* are sympatric in Tad Nam Pa. The sympatry suggests reproductive isolation, which is consistent with the present taxonomy, based on comparative morphology, which treats them as distinct species.

The diagnostic characters of the six species of Laos and *D. ranongensis* of Thailand are shown in Table 1.

Key to the species of *Dalzellia* from Laos

1a. Thallus or crustose shoot (1–)3–20 mm wide; dorsal leaves arranged in more than 2 rows ..... 6. *D. ubonensis*
1b. Thallus or crustose shoot 1–4 mm wide; dorsal leaves arranged in 1 or 2 rows 2
2a. Marginal leaves 0.4–0.5 mm long; leaves on cupule 0.1–0.4 mm long ..... 4. ***D. microphylla***
2b. Marginal leaves 0.8–2 mm long; leaves on cupule 0.3–3 mm long 3
3a. Marginal-lateral leaves shorter than dorsal leaves (ratio 0.5–0.7) ..... 2. ***D. attapeuensis***
3b. Marginal-lateral leaves equaling or longer than dorsal leaves (ratio (0.7–)1–6) 4
4a. Stamens as long as ovary; leaves on cupule monomorphic; ovules 22–32 per locule ..... 5. ***D. pseudoangustissima***
4b. Stamens longer than ovary; leaves on cupule variable; ovules (20–)30–60 per locule 5
5a. Pedicels 2–3 mm long, 1.1–1.5 times longer than ovary ..... 3. *D. kailarsenii*
5b. Pedicels 2–12 mm long, 2.5–6.5 times longer than ovary ..... 1. *D. angustissima*

1. **Dalzellia angustissima** M. Kato in Acta Phytotax. Geobot. 57: 12, f. 5. 2006.

Distribution. Laos, Thailand (SOUTHEASTERN: Trat; Kato 2006; NORTHEASTERN: Mukdahan; P. Werukamkul & L. Ampornpan, unpubl. data).

Distribution in Laos. SOUTHERN: Attapeu, Champasak, Salavan.

Habitat. Epilithic on seasonally submerged rocks in waterfalls in open place.

Notes. Dalzellia angustissima is widely and abundantly distributed in the three southern provinces of Laos, but is scarcely known in southeastern and northeastern Thailand (Kato 2006, P. Werukamkul & L. Ampornpan, unpubl. data).

The Lao specimens expand the range of variation in some characters in *D. angustissima.* The quantitative characters of the species are: shoots 1–2.5(–3) mm [1.2–2.5(–3) mm in Lao specimens], dorsal leaves 1–2 mm long (1–1.2 mm), marginal leaves 1.2–2 mm (ca. 1.2 mm), rosette leaves 0.8–2 mm (0.8–1.3 mm), pedicels 2–12 mm long (3–12 mm), stamens 1.5–2.6 mm long (same), and ovaries 1.1–2 × 0.6–1 mm (same). The specimens *LK-*

120, LK-215, LK-219, LK-239, LKF-102, LKF-108 and *LKF-114* from Laos, and *TL-1302, TL-1507* and *TKF-19* from Thailand show the same *matK* haplotype (Koi *et al*. 2012). The haplotype of *LK-418, LK-421* and *LK-437* from Laos is also the same (S. Koi, unpubl. data), but the haplotype of *LKF-111* and *LKF-123* from Laos is different.

Specimens examined (Asterisks indicates materials used in Koi *et al*. 2012). SOUTHERN LAOS. Salavan Prov.: Tad Lo, *S. Koi, R. Fujinami & T. Wongprasert LKF-114** (TNS).—Champasak Prov.: Yuang Waterfalls, *S. Koi & T. Wongprasert LK-120** (TNS); Tad Champy, *S. Koi, N. Katayama & T. Wongprasert LK-215** (TNS); Houay Pa Lai, Ban Kaeng Yao village, Bajiang District, *S. Koi & T. Wongprasert LK-219** (TNS); Houay Champy, at the point crossing Route 20, *S. Koi, R. Fujinami & T. Wongprasert LKF-102** (TNS); Tad Pha Suan Bajiang National Park, *S. Koi, R. Fujinami & T. Wongprasert LKF-108** (TNS); Tad Champy Waterfalls, *M. Kato, S. Koi & T. Wongprasert LK-437* (TNS); Huay Banglien River, Ban Lak Saosee village, *S. Koi, R. Fujinami & T. Wongprasert LKF-111** (TNS); ditto, *S. Koi, R. Fujinami & T. Wongprasert LKF-123** (TNS).—Attapeu Prov.: Tad Hiew Khon Waterfalls, Ban Muen Hua Mueang village, *S. Koi & T. Wongprasert LK-239** (TNS); Tad Nam Pa (Tad Jo) Waterfalls, Ban Xan Sai, *M. Kato, S. Koi & T. Wongprasert LK-418* (TNS); Se Pian river, Se Pian National Park, Bang Mai, *M. Kato, S. Koi & T. Wongprasert LK-421* (TNS).

2. **Dalzellia attapeuensis** Koi & M. Kato, **sp. nov.** —Fig. 1

Typus. SOUTHERN LAOS. Attapeu Province: Tad Nam Pa (Tad Jo) Waterfalls, Ban Xan Sai, 129 m, 107°03′01.7″ E, 14°56′00.0″ N, *S. Koi, N. Katayama & T. Wongprasert LK-130** (holotype TNS!, isotype HNL!).

TABLE 1. Comparison of morphological characters of species of Southeast Asian *Dalzellia*. Data from non-endemic Laos species include those from Thai specimens (Kato 2006). Diagnostic characters are indicated in bold.

	D. angustissima	*D. attapeuensis*	*D. kailarsenii*	*D. microphylla*	*D. pseudoangustissima*	*D. ranongensis*	*D. ubonensis*
Shoot width (mm)	1–2.5	1.4–4	1.5–2.5	1.3–3	1–2.5	**3-10**	**2-20**
Length of dorsal leaf (mm)	1–2	1.5–2.5	0.5–3(–4)	0.3–0.7	1–4	0.2–0.5(–2)	0.5
Length of marginal leaf (mm)	1.2–2	1–1.2	0.8–2	**0.4-0.5**	1.5–2	1–1.5(–3)	ca. 1
Relative length of marginal leaf to dorsal leaf	1–1.2	**0.5-0.7**	0.7–2.5	0.7–1.3	0.5–1.5	**3-5**	**2-6**
Form of cupule leaf*	**S**	M	**S or M****	M	M	M	M
Length of (dorsal) cupule leaf (mm)	0.3–1	0.8–1	0.3–1.5	**0.1-0.4**	1–2	0.5–1	0.3–0.9
Pedicel length (mm)	**2-12**	3–6	1.5–3	2–3.2	1.5–3	5–7	1.5–7.5
Relative length of pedicel to ovary	2.7–7.7	1.7–3	0.8–1.5	1.5–1.8	0.8–1.5	2.5–3.5	2.7–4.1
Stamen length (mm)	1.5–2.6	2.2–2.5	2–2.5	1.6–2.3	ca. 2	**ca. 3**	1.8–2
Relative length of stamen to ovary	1.1–1.4	1.2–1.3	1.1–1.3	1.2–1.3	**1**	**1.5-2**	1.1–1.6
Ovule number per locule	30–55	34–48	42–74	40–51	**22-32**	50–60	**20-39**
Relative length of capsule to width	1.8–2.2	**2.3**	1.5–2	1.8–2.1	2	1.5–2	1.5–2
Distribution***	S Laos, SE Thailand	S Laos	C Laos, NE Thailand	S Laos	N Laos	Pen Thailand	S Laos, E Thailand, S Vietnam

* M, monomorphic; S, subdimorphic.
** After Kato (2006).
*** C: Central; E: Eastern; N: Northern; NE: Northeastern; Pen: Peninsular; S: Southern; SE: Southeastern.

Description. Shoot irregularly branched, 1.5–4 mm wide; dorsal leaves linear, longer and narrower than lateral-marginal leaves, 1.5–2.5 × 0.1–0.2 mm, apex obtuse; lateral-marginal leaves narrowly deltoid, 1.2 × 0.3–0.4 mm; rosette leaves linear, 0.7–0.8 × 0.05 mm; leaves on cupule to 0.8–1 × 0.05–0.2 mm. Flower solitary; pedicel 3–6 mm long; calyx membranous, 3-lobed, lobed 1/3 to base, lobes 1.5 mm long, shorter than ovary; stamens 3, 2.2–2.5 mm long, longer than pistil, anthers ellipsoid, 0.4–0.6 × 0.3 mm; ovary 1, 3-locular, obovoid or ellipsoid, 1.8–2.0 × 0.8–0.9 mm; stigmas 3, subulate, linear or narrowly obovate, papillate, 0.3–0.4 mm long; ovules 34–48 per locule; capsules ellipsoid, ca. 1.4 × 0.6 mm, stalked (stalk 4–7 mm); ribs 9 (for the differences from closely related *D. angustissima*, see Table 1).

Distribution. Laos; SOUTHERN: Attapeu. Endemic to Laos.

Notes. The description of *Dalzellia attapeuensis* is based on a single specimen with a unique *matK* sequence, which was collected from a locality where *Dalzellia angustissima (LK-418)* occurs. It is, however, unlikely that *D. attapeuensis* is a sympatric variant of *D. angustissima*, because *D. attapeuensis* differs in the length of the cupule leaves (0.3–0.5 mm long), the pedicel (3–12 mm long), and the ovary (1.1–2 mm long).

3. **Dalzellia kailarsenii** M. Kato in Acta Phytotax. Geobot. 57: 12, f. 4. 2006.

Habitat. Epilithic on seasonally submerged rocks in waterfalls and rapids in open place.

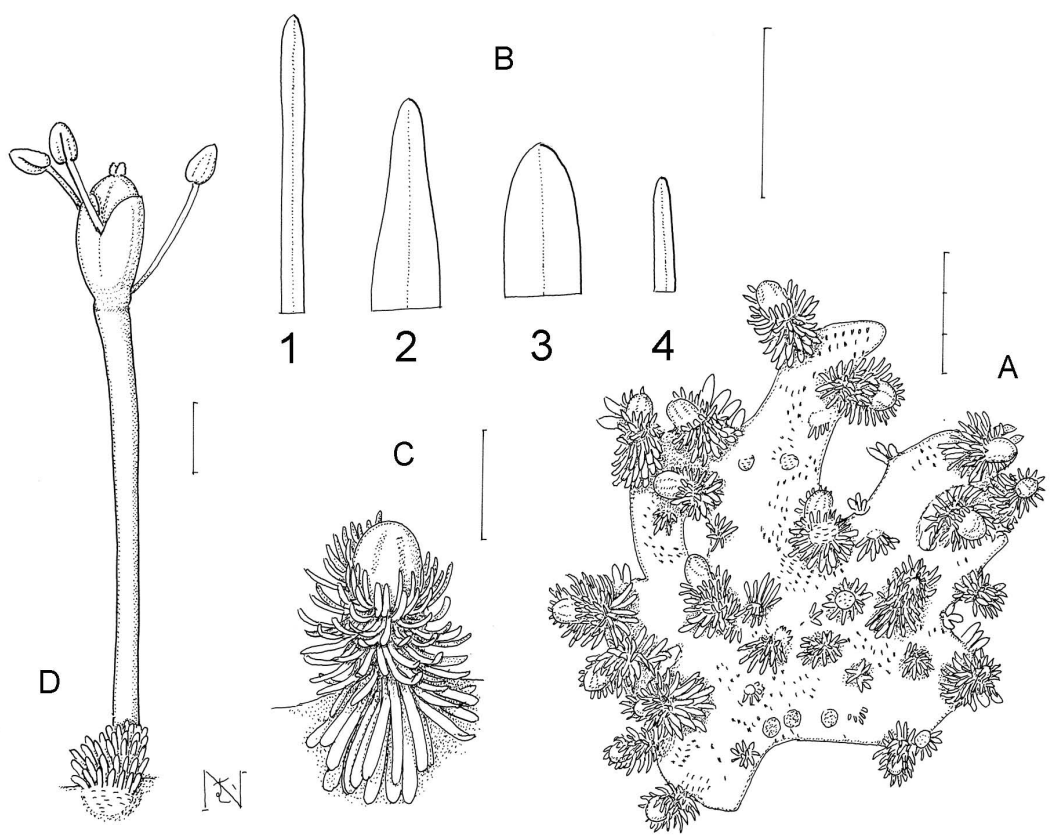

FIG. 1. *Dalzellia attapeuensis (Koi et al. LK-130).* A. Shoot with dorsal leaf scars, rosettes and cupules with flower buds. B. Leaves: 1, rosette leaf; 2, 3, marginal leaves; 4, cupule leaf. C. Flower bud enclosed by cupule with leaves of different lengths. D. Flower extending beyond cupule. Scale bars = 3 mm in A, 1 mm in B–D.

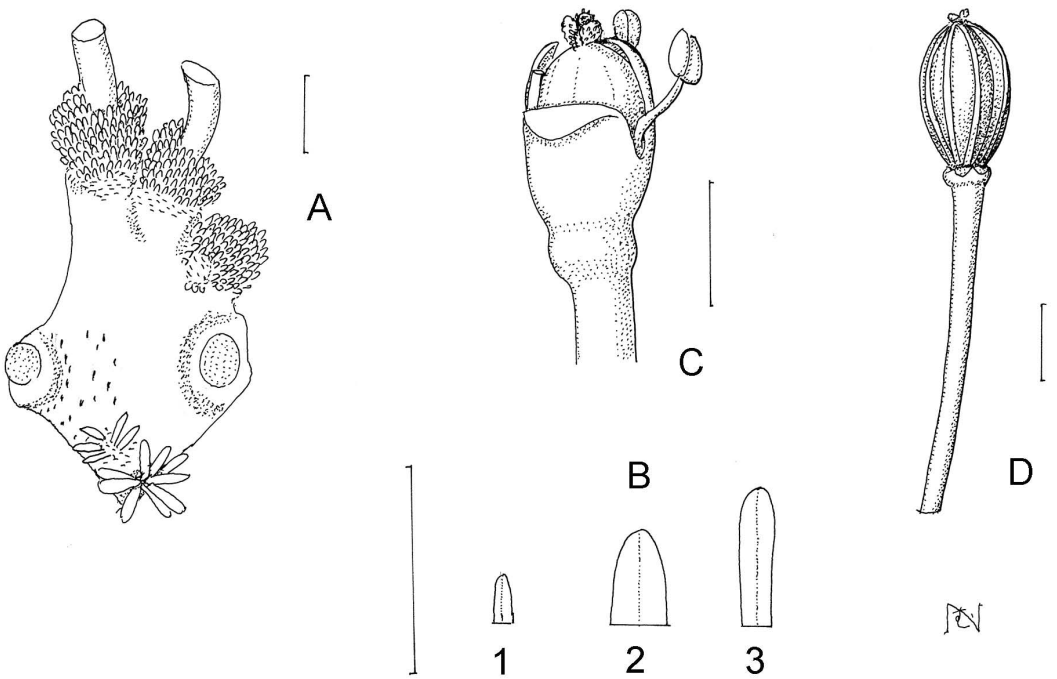

FIG. 2. *Dalzellia microphylla (Koi et al. LK-118).* A. Shoot with dorsal leaf scars, rosettes and cupules. B. Leaves: 1, cupule leaf; 2, marginal leaf; 3, rosette leaf. C. Flower. D. Fruit. Scale bars = 1 mm.

Distribution. Laos (CENTRAL: Saisombun special zone/Vientiane), Thailand (NORTHEASTERN: Chaiyaphum, Loei; Kato 2006).

Notes. Dalzellia kailarsenii in Laos differs from the type from Thailand and the protologue in the longer [0.5–1.5 mm vs. 0.3–0.5 mm in Thai material (Kato 2006)] and subdimorphic leaves on the cupule (vs. leaves apparently monomorphic), and longer pedicels (2–3 mm vs. 1.5–2 mm). We recognize that the slight differences are due to different developmental stages or geographical variation and thus are not of taxonomic importance.

Dalzellia kailarsenii is most similar to *D. angustissima* among the species with ribbon-like shoots, but differs in the longer pedicels and shorter relative length of pedicel to ovary (Table 1). The two species are distinct in molecular (*matK*) characters, and *D. kailarsenii* is sister to *D. ranongensis* (Koi *et al*. 2012).

Specimen examined. CENTRAL LAOS. Saisombun special zone/Vientiane Prov.: Ban Nam Hyam, 200 m alt., 18°21′02.2″ N, 102°42′36.2″ E, fl. fr. Jan., *M. Kato, S. Koi, C. Tsutsumi, N. Katayama, T. Wongprasert & S. Suddee L-17** (TNS).

4. **Dalzellia microphylla** Koi & M. Kato, **sp. nov.** —Fig. 2

Typus. SOUTHERN LAOS. Champasak Province: Tham Champee Waterfalls, 936 m alt., 15°12′12.5″ N, 106°07′59.2″ E, fl. fr. Jan., *S. Koi, N. Katayama & T. Wongprasert LK-118** (holotype TNS!, isotype HNL!).

Description. Shoot irregularly lobed, 1.3–3 mm wide, ribbon-like; leaf scars irregularly arranged; dorsal leaves caducous, oblong, 0.3–0.7 × 0.1–0.2 mm, narrowed to base; lateral-marginal leaves caducous, deltoid-oblong, 0.4–0.5 × 0.2–0.3 mm, apex round; rosette leaves ca. 0.6 × 0.05 mm; leaves on cupule dense, 0.1–0.4 × 0.05–0.2 mm, linear, usually narrowed to base, apex round. Flower solitary, bud enclosed by cupule 1.2–1.4 mm wide; pedicel 2–3.2 mm long; calyx 3-lobed,

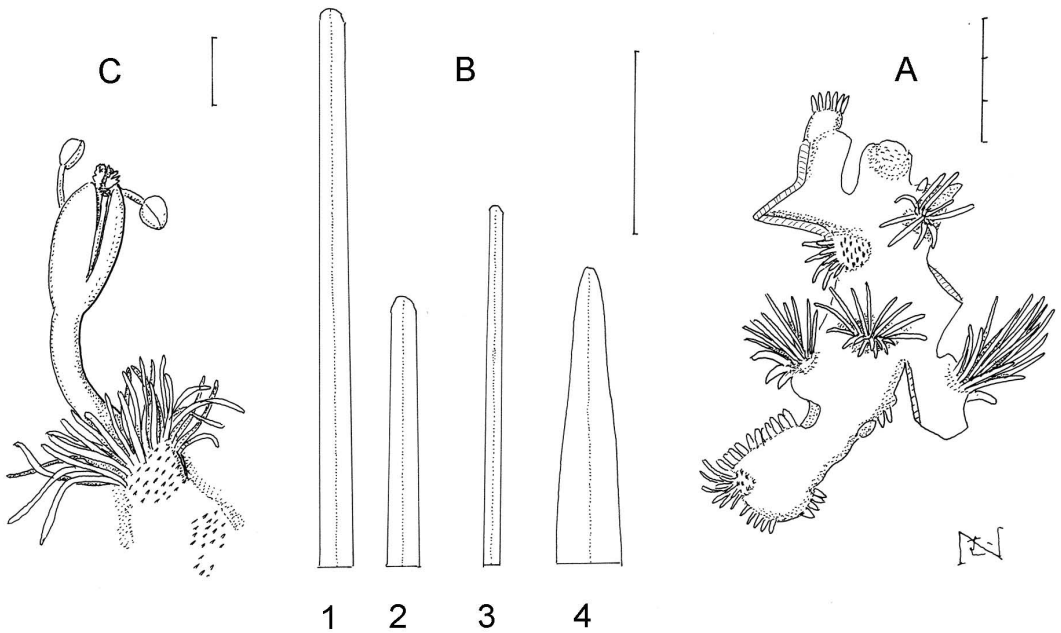

FIG. 3. *Dalzellia pseudoangustissima* (*Kato et al. L-10*). A. Shoot with rosettes and cupules. B. leaves: 1, dorsal leaf; 2, cupule leaf; 3, rosette leaf; 4, marginal leaf. C. Flower extending beyond cupule. Scale bars = 3 mm in A, 1 mm in B-C.

membranous, lobed 1/3 to base, then split more deeply, ca. 1.1–1.8 mm long; stamens 3, 1.6–2.3 mm long, longer than pistil, anthers globose or ellipsoid, 0.3 × 0.2–0.3 mm; ovary 1, 3-locular, obovoid or ellipsoid, thickest above middle, 1.3–1.8 × 0.6–1 mm; stigma 3, narrowly triangular or narrowly elliptic, papillate, 0.3–0.4 mm long; ovules borne on entire surface of septum, 40–51 per locule; capsule obovoid or ellipsoid, 1.5–1.6 × 0.7–0.9 mm, with stalk 2–4.2 mm long, 9-ribbed (for the differences from the closely related species, see Table 1).

Habitat. Epilithic on seasonally submerged rocks in waterfall in open place.

Distribution. Laos; SOUTHERN: Champasak Province, Tham Champee Waterfalls. Endemic to Laos.

Notes. Dalzellia microphylla is described from a single specimen with unique morphology (see above description and Key) and its placement in the molecular phylogeny (Koi *et al.* 2012) among the collections of *Dalzellia.*

5. **Dalzellia pseudoangustissima** Koi & M. Kato, **sp. nov.** —Fig. 3

Typus. CENTRAL LAOS. Bolikhamsai Province: Tad Leuk Waterfalls, Phuu Khao Khouay National Park, 200 m alt., 18°23′42.9″ N, 103°04′17.0″ E, fl. fr. Jan., *M. Kato, S. Koi, C. Tsutsumi, N. Katayama, T. Wongprasert & S. Suddee L-10** (holotype TNS!, isotype HNL!).

Description. Shoots adhering to rock surface, broadly ribbon-like, 1–2.5 mm wide, isotomously or anisotomously branched, leafy. Leaves subdimorphic; dorsal leaves caducous, arranged densely in often inconspicuous longitudinal rows, linear, variable in length, 1–4 × to 0.1(–0.2) mm wide, apex semicircular; marginal (lateral) leaves dense, deltoid-lanceolate, 1.5–2 × 0.2–0.5 mm, apex semicircular, facing dorsal leaves. Rosettes scattered on dorsal surface of old portions of shoots with leaf scars; rosette leaves, linear-oblong (outer leaves) to linear (inner leaves), 0.8 (outer)–3 (inner) × 0.1 (inner)–0.2 (outer) mm, apex rounded. Flowers scattered on shoot; each bud enclosed by cupule with dense filiform leaves, leaves 1–2 × ca. 0.1 mm; cupules ca. 1 mm

thick; pedicel 1.5–3(–4) mm long, usually slightly longer than ovary; calyx 3-lobed, membranous, lobed 1/3, later split more deeply, 1.5 mm long; stamens 3, ca. 2 mm long, as long as or slightly longer than ovary, anthers globular-ellipsoid, ca. 0.5 mm long, close to stigmas; ovary 1, obovoid-ellipsoid, ca. 2 × 0.8–1 mm, 3-locular, ovules 22–32 per locule, borne on whole septum surface; stigmas 3, subulate to narrowly triangular, ca. 0.2 mm long, papillate; stalk of capsule to 3 mm long, capsules ca. 2 × 1 mm, obtetrahedral, ribs 9 (for the differences from the closely related species, see Table 1).

Habitat. Epilithic on seasonally submerged rocks in waterfalls in open place.

Distribution. Laos; NORTHERN: Bolikhamsai. Endemic to Laos.

Specimens examined. CENTRAL LAOS. Bolikhamsai Prov.: Tad Xai Waterfalls, Phuu Khao Khouay National Park, 290 m alt., 18°27′18.8″ N, 103°08′31.8″ E, st. Jan., *S. Koi, R. Fujinami & T. Wongprasert LKF-12** (TNS); ditto, st. Feb., *S. Koi & T. Wongprasert LK-201** (TNS).

6. **Dalzellia ubonensis** M. Kato in Acta Phytotax. Geobot. 57: 10, f. 2. 2006.

Dalzellia ubonensis is morphologically similar to *D. ranongensis*, which is endemic to Thailand, in the markedly wide shoots and marginal leaves longer than the dorsal ones, but differs in the shape of the dorsal leaves, stamen length, and numbers of ovules. The two species, however, are phylogenetically not closely related (Koi *et al*. 2012).

Distribution. Laos, Thailand (EASTERN: Ubon Ratchathani; Kato 2006), Vietnam (SOUTHERN: Lam Dong; M. Kato, unpubl. data).

Distribution in Laos. SOUTHERN: Attapeu, Sekong.

Notes. The Lao plants of *Dalzellia ubonensis* differ morphologically from the type specimen from Thailand and the protologue. The shoots are 2–5 mm wide vs. 3–20 mm in Thai specimens and the pedicel is slightly shorter (3–7.5 mm vs. 5–8 mm). We evaluate the differences as infraspecific variation.

Specimens examined. SOUTHERN LAOS. Attapeu Prov.: Tad Hiew Khon Waterfalls, Ban Muen Hua Mueang, Jan., fl. & fr., *S. Koi, N. Katayama & T. Wongprasert LK-126** (TNS).—Sekong Prov.: Tad Fact Waterfalls, Feb., fl. & fr., *S. Koi & T. Wangprasert LK-236** (TNS).

Terniopsis H.-C. Chao in Contr. Inst. Nat. Acad. Peiping 6: 2. 1948 (publ. 1949); Chao in Acta Bot. Yunnan. 2: 296. 1980; Kato in Acta Phytotax. Geobot. 57: 18. 2006.

Fourteen species in Asia [China (Fujian), Laos, Malaysia (Peninsular), Thailand, Vietnam (Southern)] and Australia (Northern); eight or nine in Laos.

Notes. A molecular phylogenetic analysis rejected the placement of *Terniopsis* under *Tristicha* by Cook & Rutishauser (2007), and instead revealed that *Terniopsis* is sister to all other genera of Tristichoideae (Koi *et al*. 2012). Here we resurrect the genus *Terniopsis*.

Terniopsis includes parts of *Dalzellia* sensu C. Cusset & G. Cusset (1988) and *Malaccotristicha* C. Cusset & G. Cusset (Kato 2006). *Terniopsis* differs from *Dalzellia* in having subcylindrical flattened or ribbon-like roots bearing adventitious short leafy shoots called ramuli. It is similar to *Cussetia* in root morphology but differs in having two membranous bracts and the short ramuli associated with the flower.

In the *matK* phylogenetic tree of Koi *et al.* (2012), the genus *Terniopsis* comprises four subclades; 'sessilis,' 'Lao-Thai,' 'chanthaburiensis,' and 'malayana.' The 'sessilis' subclade includes *T. sessilis* from Fujian (China), *T. ubonensis* from eastern Thailand, and tentatively identified and unidentified plants from Laos. Given their phylogenetic and morphological uniqueness, two of them (*T. microstigma* and *T. vapyensis*; Table 2) are described as new. Additionally, based on the remarkable morphological features, we also describe the tentatively identified *Terniopsis* cf. *sessilis* (Koi *et al*. 2012) as another new species, *T. savannaketensis* (see Table 3 for more details), although it lacks clear genetic difference from *T. sessilis*.

The 'Lao-Thai' subclade consists of unidenti-

fied specimens from Laos and Thailand (Koi *et al*. 2012), while those from northeastern Thailand were recently described as *Terniopsis filiformis* (Werukamkul *et al*. 2012). The slight morphological differences between individuals from Laos and Thailand are considered to represent infraspecific variation.

The 'chanthaburiensis' subclade of eight haplotypes accommodates *Terniopsis chanthaburiensis* from southeastern Thailand (Koi *et al.* 2012) and specimens from southern Laos treated as *Terniopsis* cf. *chanthaburiensis.* We observed no significant morphological variation among specimens from Laos and only slight differences between the Lao and Thai specimens (see species notes). In contrast, one noteworthy specimen in our unpublished molecular phylogeny clustered within this subclade. Since it is morphologically distinguishable we describe it as a new species, *T. sesadensis* (Table 4).

The 'malayana' subclade contained species identified as *Terniopsis australis* from northern Australia, *T. brevis* from southeastern Thailand, *T. malayana* from peninsular Thailand and peninsular Malaysia, *T. minor* from southeastern Thailand, and some unidentified plants. Of these, we concluded that the Lao specimens of *Terniopsis* cf. *brevis* are conspecific with *T. brevis.* Werukamkul *et al*. (2012) described the basalmost lineage of two haplotypes, which included plants from northeastern Thailand, as *T. heterostaminata*. The Lao specimen, *LK-131,* in the lineage is morphologically identical and thus we accept *T. heterostaminata* in the flora of Laos. Samples *LKF-122, LK-124* had unique *matK* sequences (Koi *et al*. 2012), but they were excluded from this study because they have only fragmentary flowers.

Key to the species of *Terniopsis* from Laos

1a. Stamens at least 2 times as long as ovary 2
1b. Stamens as long as ovary 3
2a. Stamens 2, 2.5 times as long as ovary ..... 6. ***T. savannaketensis***
2b. Stamens 2 or 3, 2 times as long as ovary ..... 8. ***T. vapyensis***
3a. Stamens 3, rarely 2; stigmas forked, filiform at maturity ..... 3. *T. filiformis*
3b. Stamens 2; stigmas cristate 4
4a. Stigmas 0.2 mm long; relative length of ovary to width less than 1.5 ..... 5. ***T. microstigma***
4b. Stigmas more than 0.2 mm long; relative length of ovary to width more than 1.5 5
5a. Pedicel 3-14 mm long ..... 2. *T. chanthaburiensis*
5b. Pedicel < 3 mm long 6
6a. Ramuli associated with flowers 2-4, 2–6 mm long ..... 4. *T. heterostaminata*
6b. Ramulus associated with flowers 1, to 2 mm long 7
7a. Ovary ca. 2 × 0.8 mm ..... 7. ***T. sesadensis***
7b. Ovary 0.8 × 0. 5 mm ..... 1. *T. brevis*

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1. **Terniopsis brevis** M. Kato in Acta Phytotax. Geobot. 57: 22, f. 9. 2006.

Distribution. Laos, Thailand (EASTERN: Ubon Ratchathani; CENTRAL: Nakawn Nayok; PENINSULAR: Ranong; Kato 2006).

Distribution in Laos. SOUTHERN: Champasak.

Habitat. Epilithic on seasonally submerged rocks in rapids in open place.

Notes. Lao samples (*LKF-112, LK-217*), referred to as *Terniopsis* cf. *brevis* by Koi *et al.* (2012), and *LK-435* (S. Koi, unpubl. data) are here assigned to *T. brevis.* Plants from Laos differ slightly from those in Thailand in the smaller ovary (0.8 × 0.5 mm vs. 1–1.3 × 0.8 mm in Thai

TABLE 2. Comparison of morphological characters of *Terniopsis microstigma*, *T. ubonensis* and *T. vapyensis* of the 'sessilis' subclade (Koi *et al*. 2012). Character data for *T. ubonensis* are from Kato (2006). Diagnostic characters are indicated in bold.

	T. microstigma	*T. ubonensis*	*T. vapyensis*
Root width (mm)	0.6–2	**2–10**	0.8–1.2
Ramulus number	2–5	1–4	2–6
Ramulus length (mm)	1.5–3.5	**10–90**	1–5
Pedicel length (mm)	ca. 0.5*	**7–15**	2–12
Length of stalk of capsule	**1.5–3.5**	5–15	2.5–12
Stamen number	2	2, 3	2, 3
Stamen length (mm)	**ca. 1.5**	**5–6**	**3–4**
Relative length of ovary to width	1.45	1.5–2	2–2.5
Stigma length (mm)	ca. 0.2	0.5–0.7	0.2–0.6
Distribution**	S Laos	NE Thailand	S Laos

* Young pedicel.
** NE: Northeastern; S: Southern.

TABLE 3. Comparison of morphological characters of *Terniopsis savannaketensis* and *T. sessilis* with close relationships (Koi *et al*. 2012). Character data for *T. sessilis* are based on Chinese materials (Chao 1980). Diagnostic characters are indicated in bold.

	T. savannaketensis	*T. sessilis*
Root width (mm)	0.6–4	1–1.5
Ramulus length (mm)	**1–3**	**7–9**
Flower number per flowering shoot	1–4	1–2
Calyx length (mm)	**1.2–1.5**	**ca. 2.5**
Stamen number	2	2, 3
Stamen length (mm)	**3–5**	**0.9–2.5**
Ovary length (mm)	**1.2–2**	**0.6–0.8**
Capsule-stalk length (mm)	0.5–5.5	ca. 1
Distribution	North Central Laos	Southeast China

plants), but more ovules (20–25 per locule vs. 13–20), and shorter stalk of the capsule (1–1.2 mm vs. to 3.5 mm). We recognize the differences as infraspecific variation.

Specimens examined. (Asterisks indicate materials used in Koi *et al*. 2012). SOUTHERN LAOS. Champasak Prov.: Tad Champy, 137 m alt., 15°17′41.0″ N, 105°51′36.6″ E, st. Feb., *S. Koi & T. Wongprasert LK-217** (TNS); Tad Champy Waterfalls, 137 m alt., 105°51′36.6″ E, 15°17′41″ N, *M. Kato, S. Koi & T. Wongprasert LK-435* (TNS); Huay Banglieng river, Ban Lak Saosee village (= Ban Lak See), 86 m alt., 14°58′51.4″ N, 105°54′56.2″ E, st. Jan., *S. Koi, R. Fujinami & T. Wongprasert LKF-112** (TNS).

2. **Terniopsis chanthaburiensis** M. Kato & Koi in Gard. Bull. Singapore 61: 56, f. 1. 2009.

Distribution. Laos, Thailand (SOUTHEASTERN: Chanthaburi; Kato 2006).

Distribution in Laos. SOUTHERN: Salavan, Champasak.

Habitat. Epilithic on seasonally submerged rocks in rapids in open place.

TABLE 4. Comparison of morphological characters of sister taxa *Terniopsis sesadensis* and *T. chanthaburiensis* (Koi *et al.* 2012, S. Koi, unpubl. data). Character data for *T. chanthaburiensis* include those from Thai specimens used in Kato & Koi (2009). Diagnostic characters are indicated in bold.

	T. chanthaburiensis	*T. sesadensis*
Root width (mm)	0.2–1	ca. 0.8
Number of ramuli in vegetative shoot	**5–7**	**1–2**
Number of flowers per flowering shoot	1–4	1
Number of ramuli per flowering shoot	1–11	1–3
Length of ramuli in flowering shoot (mm)	**4–23**	**ca. 0.6**
Pedicel length (mm)	**2–10**	**1.3–1.8**
Stamen length (mm)	1.2–2.2	1.5–2
Distribution*	S Laos, SE Thailand	S Laos

* S: Southern; SE: Southeastern.

Notes. The Lao specimens are identical to or similar to the type specimen from Thailand and agree with the protologue in the width of the root, the length and branching time of the ramuli, the length of the pedicel and capsule stalk, the number and length of the stamens, and the size of the ovary. They differ from the Thai plants only in the longer ramuli associated with flowers (23 mm vs. to 5 mm in Thai specimens) and the smaller ovary (1–1.2 × 0.5–0.9 mm vs. ca. 2 × ca. 1 mm). We recognize them as conspecific.

Terniopsis chanthaburiensis is similar to *T. savannaketensis* in the multiple (1–3 vs. 1–4) flowers per shoot on the thin root, longer ramuli in the flowering shoot, shorter pedicel, smaller stamens, and smaller ovary.

Terniopsis chanthaburiensis occurs disjunctly in Laos and Thailand, but is more abundant in Laos.

Specimens examined. SOUTHERN LAOS. Salavan Prov.: Huay Taphung River, at the point crossing Route 20, 514 m alt., 15°27′59.7″ N, 106°10′12.3″ E, st. Jan., *S. Koi, R. Fujinami & T. Wongprasert LKF-117** (TNS); Nam Dong, Ban Mai village, 186 m alt., 15°42′16.7″ N, 106°18′54.6″ E, st. fl. fr. Feb., *S. Koi & T. Wongprasert LK-227** (TNS); Nam Thone stream, Ban Chone village, 187 m alt., 15°41′43.4″ N, 106°15′58.5″ E, st. fl. fr. Feb., *S. Koi & T. Wongprasert LK-228** (TNS); Sesad River, Ban Viangxai village, 200 m alt., 15°42′0.5″ N, 106°14′06.6″ E, st. Feb., *S. Koi & T. Wongprasert LK-229** (TNS); Sesad River, Ban Bueng Kham, 171 m alt., 15°42′25.2″ N, 106°08′36.5″ E, st. fl. fr. Feb., *S. Koi & T. Wongprasert LK-231** (TNS); Se Don River, 105°58′25.9″ E, 15°41′56.9″ N, 122 m alt., Ban Saphad, *M. Kato, S. Koi & T. Wongprasert LK-402* (TNS); Huay Tapung stream at border between Vapy Dist. and Salavan Dist., Ban Huay Tapungm, Vapy Dist., 160 m alt.,106°06′33.7″ E, 15°41′24.2″ N, *M. Kato, S. Koi & T. Wongprasert LK-407* (TNS); Se Sad River, opposite side to a temple, about 20 km from Salavan, Ban Bueng Sai, 167 m alt., 106°13′45.2″ E, 15°42′19.9″ N, *M. Kato, S. Koi & T. Wongprasert LK-410b* (TNS).—Champasak Prov.: Houay Champy River, at the point crossing Route 20, 186 m alt., 15°15′30.6″ N, 105°55′59.5″ E, st. Jan., *S. Koi et al. LKF-101** (TNS); ditto, fl. fr. Feb., *S. Koi & T. Wongprasert LK-212** (TNS); Se Don River, along Route 13, 188 km from Savannakhet, 105°45′54.1″ E, 15°28′57.7″ N, 135 m alt., Ban Huay Xao, *M. Kato, S. Koi & T. Wongprasert LK-401* (TNS).

3. **Terniopsis filiformis** Werukamkul, Ampornpan, Koi & M. Kato in Acta Phytotax. Geobot. 63: 17, f. 3. 2012.

Distribution. Laos (CENTRAL: Khammouane, Savannakhet; SOUTHERN: Salavan, Sekong, Champasak, Attapeu), Thailand (NORTHEASTERN: Loei; Werukamkul *et al.* 2012).

Habitat. Epilithic on seasonally submerged rocks in waterfall in open place.

Notes. The Lao specimens differ from Thai specimens in the longer pedicel (1–14 mm vs. 1–2.9 mm in the latter), but the range of variation overlaps in most other characters described in the protologue (Werukamkul *et al.* 2012). The plants

in both countries are therefore conspecific.

Terniopsis filiformis is more widely distributed in Laos than in Thailand.

Specimens examined. CENTRAL LAOS. Khammouane Prov.: Tad Namsanam Waterfalls, Ban Khounkham, Ban Namsanam Hinboun Dist., 260 m alt., 18°13′11.2″ N, 104°30′21.6″ E, st. fl. fr. Jan., *S. Koi, R. Fujinami & T. Wongprasert LK-112** (TNS).—Savannakhet Prov.: stream on the way to Tad Salaen, 251 m alt., 16°40′05.9″ N, 106°25′43.2″ E, fl. fr. Feb., *S. Koi & T. Wongprasert LK-206** (TNS). Southern Laos. Salavan Prov.: Sedon River, Salavan, 176 m alt., 15°43′14.2″ N, 106°25′47.8″ E, st. fl. fr. Feb., *S. Koi & T. Wongprasert LK-225** (TNS); Sedon River, Ban Phonebok village, 176 m alt., 15°42′26.6″ N, 106°26′11.2″ E, fl. Feb., *S. Koi & T. Wongprasert LK-226** (TNS); Kaeng Koo rapid, Vapy Dist., 141 m alt., 15°42′31.7″ N, 106°04′08.1″ E, fl. fr. Feb., *S. Koi & T. Wongprasert LK-234** (TNS); Nam Tha river, Ban Soptout, Luang Namtha, Laos, *S. Koi, N. Katayama & T. Wongprasert LK-311** (TNS); Se Nam Mana river, Ban Nam, 190 m alt., 15°57′45.4″ N, 106°20′20.2″ E, *M. Kato, S. Koi & T. Wongprasert LK-409* (TNS).—Sekong Prov.: Tat Hia Waterfalls, 178 m alt., 15°19′47.2″ N, 106°40′41.5″ E, st. fl. fr. Feb., *S. Koi & T. Wongprasert LK-235* (TNS)*.—Champasak Prov.: Tad Champy Waterfalls, 137 m alt., 15°17′41.0″ N, 105°51′36.6″ E, st. Feb., *S. Koi & T. Wongprasert LK-216** (TNS); Houay Pa Lai River, Ban Kaeng Yao, Bajiang, *S. Koi & T. Wongprasert LK-218B1**; ditto, *S. Koi & T. Wongprasert LK-218B2** (TNS); Tad Champy Waterfalls, 137 m alt., 105°51′36.6″ E, 15°17′41″ N, *M. Kato, S. Koi & T. Wongprasert LK-436* (TNS).—Attapeu Prov.: Sekong River, Kaeng Mueang, Lavy village, 106 m alt., 15°18′03.3″ N, 106°42′43.3″ E, st. fl. Jan., *S. Koi et al. LK-133** (TNS); ditto, st. fl. fr. Feb., *S. Koi & T. Wongprasert LK-240** (TNS); Se Khong river, Ban Mitsamphan, Sanamsay Dist., 71 m alt., 14°40′40.2″ N, 106°34′59.2″ E, *M. Kato, S. Koi & T. Wongprasert LK-420* (TNS); Se Kaman River, 141 m alt., 107°6′46″ E, 14°53′28.1″ N, *M. Kato, S. Koi & T. Wongprasert LK-430* (TNS); Se Lamong stream, Dong Ampham National Park, 178 m alt., 107°16′6.3″ E, 14°44′40.9″ N, *M. Kato, S. Koi & T. Wongprasert LK-431* (TNS).

4. **Terniopsis heterostaminata** Werukamkul, Ampornpan, Koi & M. Kato in Acta Phytotax. Geobot. 63: 15. f. 2, 2012.

Distribution. Laos (SOUTHERN: Salavan, Attapeu), Thailand (NORTHEASTERN: Loei; Werukamkul *et al*. 2012).

Habitat. Epilithic on seasonally submerged rocks in waterfalls in open place.

Notes. The ranges of variation in the quantitative features of *T. heterostaminata* in Laos overlap with those in plants from Thailand (Werukamkul *et al*. 2012). Although the stamens are at most subequal, not obviously heteromorphic in plants of Laos, the other characters are shared by the Lao and Thai plants. Therefore we treat the Lao plants as *T. heterostaminata*.

Specimens examined. SOUTHERN LAOS. Salavan Prov.: Se Sad River, opposite side to a temple, about 20 km from Salavan, Ban Bueng Sai, 167 m alt., 106°13′45.2″ E, 15°42′19.9″ N, *M. Kato, S. Koi & T. Wongprasert LK-410a* (TNS); Se Sad River, near a school and temple, Ban Bueng Sai, 200 m alt., 106°14′06.6″ E, 15°42′0.5″ N, *M. Kato, S. Koi & T. Wongprasert LK-411a,b* (TNS).—Attapeu Prov.: Tad Nam Pa (Tad Jo) Waterfalls, Ban Xan Sai, 129 m alt., 14°56′0.0″ N, 107°03′01.7″ E, st. fl. fr. Jan., *S. Koi, R. Fujinami & T. Wongprasert LK-131** (TNS); Se Lamong stream, Ampham National Park, 178 m alt., 107°16′06.3″ E, 14°44′40.9″ N, *M. Kato, S. Koi & T. Wongprasert LK-431c* (TNS); ditto, *M. Kato, S. Koi & T. Wongprasert LK-432* (TNS); Tad Sa Mong Phak Waterfalls, Se Pian National Park, 120 m alt., 106°26′39.2″ E, 14°45′01.2″ N, *M. Kato, S. Koi & T. Wongprasert LK-424* (TNS).

5. **Terniopsis microstigma** Koi & M. Kato, **sp. nov.** —Fig. 4

Typus. SOUTHERN LAOS. Salavan Province: Se Sad River, near a school and temple, Ban Bueng Sai District, 200 m alt., 106°14′6.6″ E, 15°42′0.5″ N, st. fl. Feb., *M. Kato, S. Koi & T. Wongprasert LK-412* (holotype TNS!, isotype HNL!).

Description. Root flattened-subcylindrical, 0.6–2 mm wide, monopodially branched; ramuli on both flanks of root, 1.5–3.5 mm long, unbranched or 1 time branched; leaves in 3 ranks, imbricate, middle leaf round, 0.4–0.8 × 0.5–0.6 mm, lateral leaf elliptic, 0.4–0.8 × 0.3–0.5 mm. Flowering shoots on both flanks of root, single flower associated with 2–5 ramuli, ramuli 1.5–2.5 mm long; bracts 2, at base of pedicel, broadly ovate, ca. 1 mm long, 1.5–2 mm wide; pedicels (when young) ca. 0.5 mm long, perhaps longer at maturity; calyx membranous, 3-lobed ca. 1/3 from tip, ca. 1.5 × ca. 0.9 mm; stamens 2, ca. 1.5 mm long in bud; anthers ellipsoid, ca. 1 mm long; ovary 1, sessile, 3-locular, obovoid, ca. 1.3 × ca.

0.9 mm, stigmas 3, cristate, ca. 0.2 mm long; ovules 9–17 per locule, borne on nearly whole septum surface, stalk of capsule 1.5–3.5 mm long, capsules obovoid, 1.3–2 × 1–1.2 mm, 9-ribbed (for the differences from the closely related species, see Table 2).

Distribution. Laos; SOUTHERN: Salavan. Endemic to Laos.

Habitat. Epilithic on seasonally submerged rocks in waterfalls in open places.

Specimens examined. SOUTHERN LAOS. Salavan Prov.: Tad Lo waterfall, 369 m alt., 18°03′28.0″ N, 106°16′22.3″ E, st. Jan., *S. Koi et al. LKF-113** (TNS); Sesad river, Ban Viangxai village, 200 m alt., 15°42′00.5″ N, 106°14′06.6″ E, st. (fl. fr.) Feb., *S. Koi & T. Wongprasert LK-230** (TNS).

6. **Terniopsis savannaketensis** Koi & M. Kato, **sp. nov.** —Fig. 5

Typus. CENTRAL LAOS. Savannakhet Province: Sammataek rapid, Muang Phin District, 150 m alt., 16°18′03.4″ N, 105°58′56.8″ E, *S. Koi & T. Wongprasert LK-210** (holotype TNS!, isotype HNL!).

Description. Root flattened-subcylindrical to ribbon-like, 0.6–4 mm wide, monopodially branched; ramuli on both flanks of root, 1–3 mm

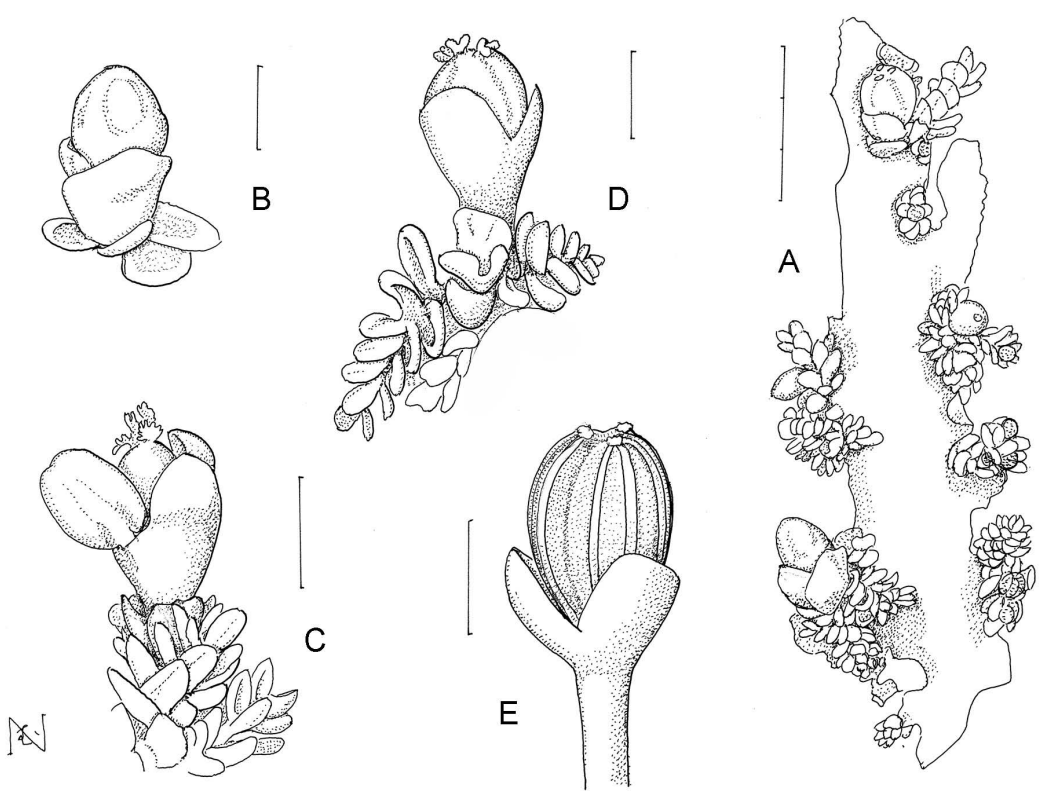

FIG. 4. *Terniopsis microstigma* (*Kato et al. LK-412*). A. Root with flower buds and ramuli on flank. B. Flower bud subtended by bracts. C, D. Flowers and subtending ramuli. E. Fruit. Scale bars = 3 mm in A, 1 mm in B–E.

long, 1–4 times branched; leaves in 3 ranks, imbricate, middle leaf round-ovate, 0.4–0.7 × 0.4–0.5 mm, lateral leaf elliptic, 0.4–0.5 × 0.3–0.4 mm. Flowering shoots on both flanks of root, 1–4 flowers per shoot, associated with 1-several ramuli; ramuli 1.2–4 mm long; bracts 2, at base of pedicel, ovate or broadly ovate, 1–2 × 1–2 mm, thick, firm; pedicels 0.8–2.5 mm long; calyx membranous, 3-lobed 1/3–1/2 from tip, 1.2–1.5 mm long, as long as ovary; stamens 2, 3–5 mm long, much longer than pistil; anthers ellipsoid, ca. 0.9–1.1 mm long; ovary 1, sessile, 3-locular, obovoid or ellipsoid, 1.2–2 × 0.8–1 mm, stigmas 3, cristate, 0.3–0.8 mm long; ovules 2–10 per locule, borne on whole septum surface except small central area; stalk of capsules 0.5–5.5 mm long, capsule obovoid to ellipsoid, 1.1–2 × 0.8–1 mm, 9-ribbed (for the differences from closely related *T. sessilis*, see Table 3).

Distribution. Laos; South CENTRAL: Savannakhet. Endemic to Laos.

Habitat. Epilithic on seasonally submerged rocks in waterfalls in open places.

Notes. The molecular data from one of the three haplotypes of *Terniopsis savannaketensis* are identical to those of *T. sessilis* from Fujian, China (Koi *et al*. 2012). Nonetheless, *T. savannaketensis* is morphologically well defined (Table

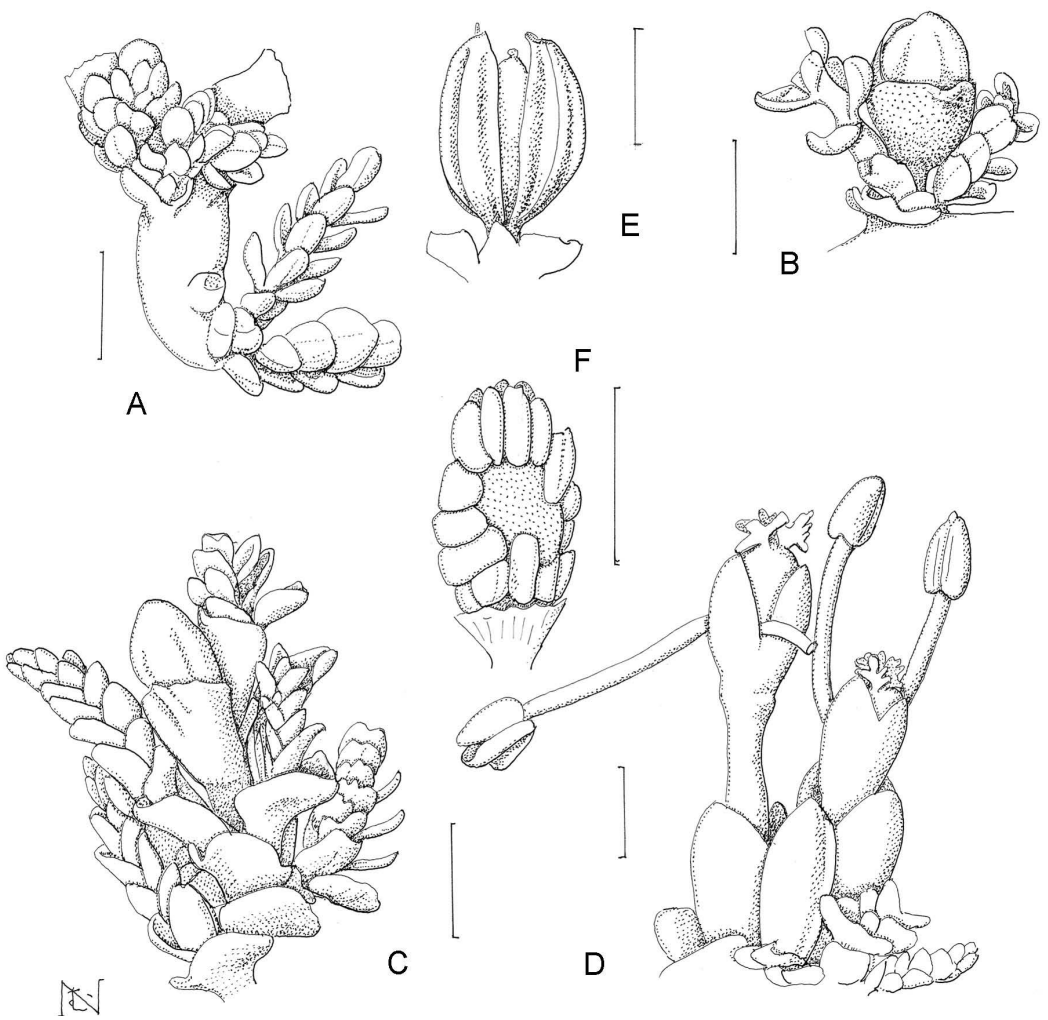

FIG. 5. *Terniopsis savannaketensis* (A, B, *Koi & Wongprasert LK-205*; C–F, *Koi & Wongprasert LK-210*). A. Ramuli on flank of root. B. Flower bud subtended by bracts with ramuli. C. Flowering shoot with several ramuli. D. Flowers. E. Dehiscing fruit. F. Ovules on septum with central sterile part. Scale bars = 1 mm.

3). The identical haplotypes are probably due to incomplete lineage sorting. The geographic disjunction between China and Laos may be due to long distance dispersal.

Specimens examined. CENTRAL LAOS. Savannakhet Prov.: Tad Sakhoy rapid, 174 m alt., 16°43′04.1″ N, 106°14′13.3″ E, st. fl. fr. Jan., *S. Koi & T. Wongprasert LK-205** (TNS); Tad Hai Waterfalls, Ban Hai, Muang Phin Dist., 139 m alt., 16°16′47.8″ N, 105°57′25.1″ E, st. fl. fr. Jan., *S. Koi & T. Wongprasert LK-209** (TNS).

7. **Terniopsis sesadensis** Koi & M. Kato, **sp. nov.** —Fig. 6

Typus. SOUTHERN LAOS. Salavan Province: Se Sad River, opposite side to a temple, about 20 km from Salavan, Ban Bueng Sai, 167 m alt., 106°13′45.2″ E, 15°42′19.9″ N, *M. Kato, S. Koi & T. Wongprasert LK-410bc* (holotype TNS!, isotype HNL!).

Description. Root subcylindrical, ca. 0.8 mm wide, monopodially branched; ramuli on both flanks of root, to 4 mm long, unbranched or 1 time branched; leaves in 3 ranks, close or imbricate, middle leaf ovate, to 0.8 × 0.5 mm, lateral leaf elliptic, to 0.6 × 0.3 mm. Flowering shoots on both flanks of root, flower 1, associated with 1–3(–5) ramuli, ramuli ca. 2 mm long; bracts 2, at base of pedicel, round, 1.3 × 1.5 mm; pedicel ca. 1.3–1.8 mm long; calyx membranous, 3-lobed 1/4 from tip, later split more deeply, 1.8 mm long, as long as pistil; stamens 2, ca. 1.5 mm long, as long as ovary, anthers 0.3 mm long; ovary 1, sessile or stalked (stalk to 1 mm long), 3-locular, narrowly obovoid, 1.3–1.5 × 0.7–0.9 mm; stigmas 3, cristate; ovules ca. 16 per locule, on nearly entire septum; stalk of capsule 1.5–2 mm long; capsule 1.3–1.8 × 0.9–1.2 mm, trigonous, 9-ribbed (for the differences from closely related *T. chanthaburiensis*, see Table 4).

Distribution. Laos; SOUTHERN: Salavan. Endemic to Laos.

Notes. Terniopsis sesadensis is sister to *T. chanthaburiensis* (S. Koi, unpubl. data). The two species form the ‘chanthaburiensis’ subclade, sensu Koi *et al*. (2012). The description is based on a single specimen.

8. **Terniopsis vapyensis** Koi & M. Kato, **sp. nov.** —Fig. 7

Typus. SOUTHERN LAOS. Salavan Province: Kaeng Koo rapid, Vapy District, 141 m alt., 15°42′31.7″ N, 106°04′08.1″ E, *S. Koi & T. Wongprasert LK-233** (holotype TNS!, isotype HNL!)

Description. Root flattened-subcylindrical, with conspicuous root cap, 0.8–1.2 mm wide, monopodially branched; ramuli on both flanks of root, 1–5 mm long, several times branched; leaves in 3 ranks, imbricate, middle leaf round, ca. 0.5 × ca. 0.5 mm, lateral leaf oblong-elliptic or round-ovate, 0.5–0.6 × 0.3–0.5 mm. Flowering shoots on both flanks of root; flower 1, associated with 2–6 ramuli; ramuli 1.3–10 mm long; bracts 2, at base of pedicel, broadly ovate, 0.9–1.4 × 1–2 mm; pedicels 2–12 mm long; calyx membranous, 3-lobed ca. 1/3 from tip, later split more deeply, ca. 1.5 mm long, as long as or slightly longer than ovary; stamens 2 or 3, 3–4 mm long, about 2× as long as ovary; anthers ellipsoid, 0.8–1 mm long; ovary 1, sessile, 3-locular, ellipsoid or obovoid-ellipsoid, 1.5–1.8 × 0.6–0.9 mm, stigmas 3, cristate, 0.2–0.6 mm long; ovules 7–11 per locule, covering nearly entire septum surface, stalk of capsules 2.5–12 mm long; capsules ellipsoid or obovoid-ellipsoid, 1.4–2.2 × ca. 1 mm, 9-ribbed (for the differences from the closely related species, see Table 2).

Distribution. Laos; SOUTHERN: Salavan. Endemic to Laos.

Habitat. Epilithic on seasonally submerged rocks in waterfalls in open places.

Notes. Terniopsis vapyensis is sister to *T. ubonensis* of the same ‘sessilis’ subclade (Koi *et al.* 2012) and morphologically differs from it (Table 2). It is similar to *T. brevis* of Laos and Thailand and *T. minor* of Thailand, both belonging to the ‘malayana’ subclade, but differs in having stamens longer than the ovaries versus stamens as long as the ovaries.

Specimens examined. SOUTHERN LAOS. Salavan Prov.: Se Don River, Ban Lao, 119 m alt., 15°41′55.8″ N, 106°01′44.4″ E, *M. Kato, S. Koi & T. Wongprasert LK-403* (TNS); ditto, *M. Kato, S. Koi & T. Wongprasert LK-403b* (TNS); Kaeng Koo rapid, Vapy Dist., 141 m alt., 15°42′31.7″ N, 106°04′08.1″ E, *M. Kato, S. Koi & T. Wong-*

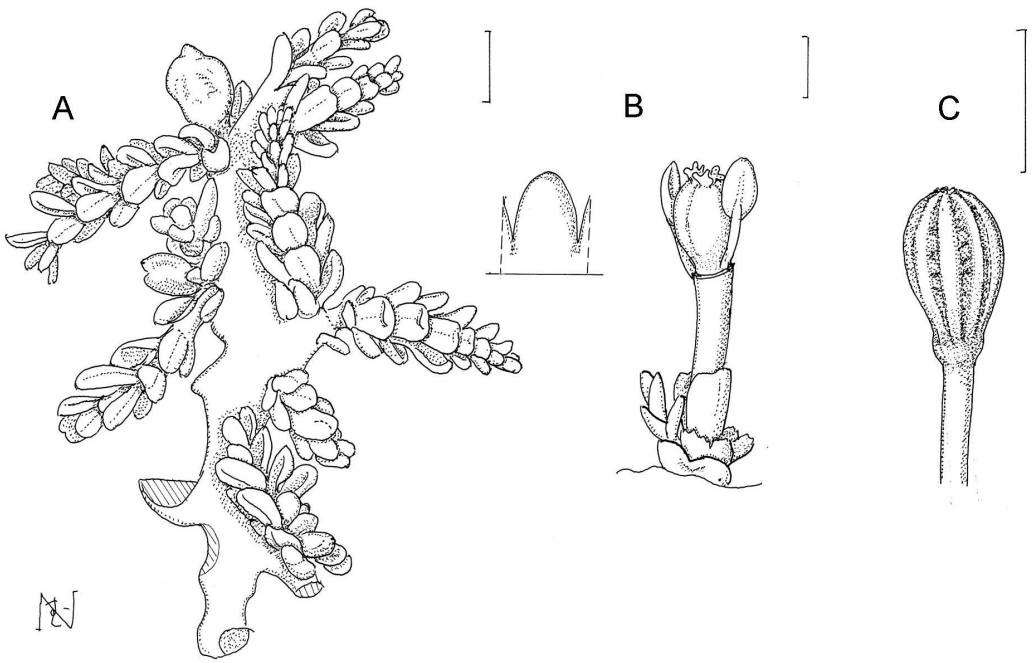

FIG. 6. *Terniopsis sesadensis* (*Kato et al. LK-410bc*). A. Root with flower bud and ramuli on flank. B. Flower (calyx removed) and part of detached calyx (left). C. Fruit. Scale bars = 1 mm.

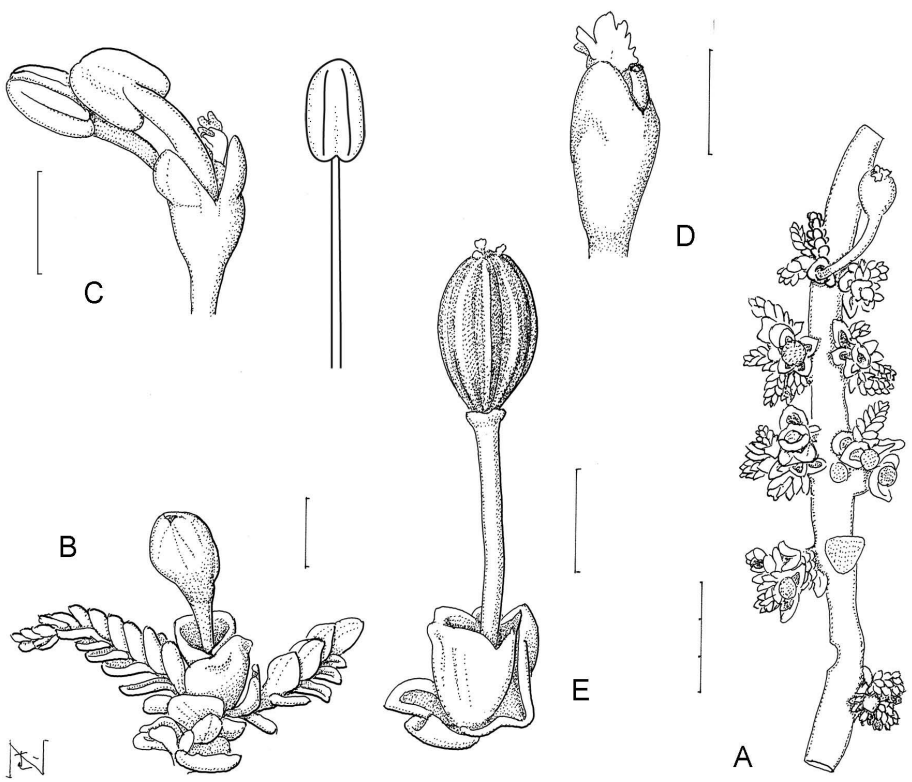

FIG. 7. *Terniopsis vapyensis* (*Koi & Wongprasert LK-233*). A. Root with ramuli and flower, flower scars and ramuli on flank. B. Young flower subtended by bracts and ramuli. C. Young flower and mature stamen. D. Flower with cristate stigmas and lower part of filament (distal part of stamen fallen). E. Fruit. Scale bars = 3 mm in A, 1 mm in B–E.

TABLE 5. Comparison of Tristichoideae by country in Asia.

	Laos	Thailand	Cambodia	Vietnam	Malaysia	China	Australia	India	Sri Lanka
Cussetia carinata	+	−	+	−	−	−	−	−	−
Cussetia diversifolia	−	+	−	−	−	−	−	−	−
Dalzellia angustissima	+	+	−	−	−	−	−	−	−
Dalzellia attapeuensis	+	−	−	−	−	−	−	−	−
Dalzellia kailarsenii	+	+	−	−	−	−	−	−	−
Dalzellia microphylla	+	−	−	−	−	−	−	−	−
Dalzellia pseudoangustissima	+	−	−	−	−	−	−	−	−
Dalzellia ranongensis	−	+	−	−	−	−	−	−	−
Dalzellia ubonensis	+	+	−	+	−	−	−	−	−
Dalzellia zeylanica	−	−	−	−	−	−	−	+	+
Indodalzellia gracilis	−	−	−	−	−	−	−	+	−
Indotristicha ramosissima	−	−	−	−	−	−	−	+	−
Indotristicha tirunelveliana	−	−	−	−	−	−	−	+	−
Terniopsis australis	−	−	−	−	−	−	+	−	−
Terniopsis brevis	+	+	−	−	−	−	−	−	−
Terniopsis chanthaburiensis	+	+	−	−	−	−	−	−	−
Terniopsis filiformis	+	+	−	−	−	−	−	−	−
Terniopsis heterostaminata	+	+	−	−	−	−	−	−	−
Terniopsis malayana	−	+	−	−	+	−	−	−	−
Terniopsis microstigma	+	−	−	−	−	−	−	−	−
Terniopsis minor	−	+	−	−	−	−	−	−	−
Terniopsis ramosa	−	+	−	−	−	−	−	−	−
Terniopsis savannaketensis	+	−	−	−	−	−	−	−	−
Terniopsis sesadensis	+	−	−	−	−	−	−	−	−
Terniopsis sessilis	−	−	−	−	−	+	−	−	−
Terniopsis ubonensis	−	+	−	−	−	−	−	−	−
Terniopsis vapyensis	+	−	−	−	−	−	−	−	−
No. of species and endemics in parentheses	15(7)	13(6)	1(0)	1(0)*	1(0)	1(1)	1(1)	4(3)	1(0)

+, present; −, absent.
* Probably two additional species.

prasert LK-404, LK-404d (TNS); ditto, *M. Kato, S. Koi & T. Wongprasert LK-405b, LK-405c, LK-405d* (TNS); Kaeng Krata rapid, Se Don River, at the point crossing road from Salavan to Tahoy, Ban Tha Khaek, 130 m alt., 15°45′16.9″ N, 106°22′12.6″ E, *M. Kato, S. Koi & T. Wongprasert LK-408a* (TNS); ditto, *M. Kato, S. Koi & T. Wongprasert LK-408b* (TNS).

Characteristic of Tristichoideae in Laos

Laos harbors at least 15 species in three genera of Tristichoideae. At both the genus and species levels there is high similarity with Thailand, where all the genera and seven out of the 15 species occur (Table 5). The Tristichoideae of Cambodia and Vietnam show slight overlap with Laos, with only *Cussetia carinata* in Cambodia and *Dalzellia ubonensis* in Vietnam (Table 5).

The Tristichoideae of Laos exhibit high endemism (7 out of 15 species; 47%), comprising four species of *Terniopsis* and three species of *Dalzellia* (Table 5). The incidence of endemism is comparable to Thailand, where 6 of 13 species, 46%, are endemic (Kato 2006, Kato & Koi 2009, Werukamkul *et al*. 2012). Laos and Thailand thus represent a center of diversity for Tristichoideae in Asia.

We thank T. Wongprasert, S. Suddee, C. Tsutsumi, R. Fujinami, and N. Katayama for their help in the field studies, Y. Hirayama for her technical assistance, anonymous reviewers for providing useful suggestions for the manuscript, and D. E. Boufford for the linguistic corrections. We are also indebted to the curators of the herbaria of the National Museum of Natural History, Paris (P), and the

National Museum of Nature and Science, Tsukuba (TNS) for help in examining specimens on loan and those deposited in the TNS herbarium. This study was in part supported by Grants-in-Aid (KAKENHI) for Scientific Research (No. 26870502, 25291091) from the Japan Society for the Promotion of Science (JSPS).

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Received May 26, 2014; accepted February 23, 2015